



Echinoderm diversity of a tropical estuary in the largest river basin of the Costa Rican Pacific, Eastern Tropical Pacific

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Abstract. Echinoderms within the Eastern Tropical Pacific have mainly been studied in association with coral reefs. Investigations on echinoderms associated with soft-bottoms and estuaries are still scarce. The present study reports on the echinoderm species inhabiting the soft-bottom sediments of shallow-brackish waters adjacent to the largest river basin along the Pacific coast of Costa Rica, Térraba-Sierpe wetland. Nine species were recorded, three of them new records for Costa Rica: *Luidia columbia*, *L. latiradiata*, and *L. superba*. The most common species were *L. columbia*, *Astropecten armatus*, *A. regalis*, and *L. latiradiata*. This contributes towards current knowledge on the biodiversity of Térraba-Sierpe wetland and should be considered as a baseline upon which to monitor the effects of future impacts on this important mangrove area.

Key words. New records; marine biodiversity; Echinodermata; Asteroidea; *Luidia latiradiata*; wetland; Térraba-Sierpe

INTRODUCTION

Echinoderms are a diverse group of marine invertebrates, currently comprised of approximately 7000 known species (PAWSON 2007; APPELTANS et al. 2012). They play a key role in shallow-water habitats as herbivores, organic matter recyclers and predators of several benthic organisms (JANGOUX 1982; JANGOUX & LAWRENCE 1982; MENGE 1982; BIRKELAND 1989). This mainly marine group is one of the most common and conspicuous in littoral environments across all latitudes, including the tropics (LAWRENCE 1987).

A high diversity of echinoderms (597 species) inhabits the Eastern Tropical Pacific (ETP) (PÉREZ-RUZAFÁ et al. 2013). Echinoderm fauna had been recently studied within the ETP and species lists were generated for: Gulf of California (SOLÍS-MARÍN et al. 2005), Tropical Mexican Pacific (BENÍTEZ-VILLALOBOS et al. 2008; HONEY-ESCANDÓN et al. 2008, GRANJA-FERNÁNDEZ et al. 2015), El Salvador (BAR-

RAZA & HASBÚN 2005), Panamic Pacific (LESSIOS 2005), and Colombian Pacific (NEIRA & CANTERA 2005). However, some regions like the Pacific coast of Central America remain poorly studied and the geographic distribution ranges remain unknown for some species in the ETP (ALVARADO et al. 2013).

In Costa Rica, echinoderms have been studied sporadically (ALVARADO & CORTÉS 2009). A total of 183 species have been reported for the Pacific coast (ALVARADO et al. 2013). Most studies focused on echinoderms associated with coral reefs: Cocos Island (DEICHMANN 1941, 1958; CLARK 1948; HERTLEIN 1963; GUZMÁN & CORTÉS 1992; LESSIOS et al. 1996; GUZMÁN & CORTÉS 2007; ALVARADO & CHIRIBOGA 2008), Culebra Bay (ALVARADO 2008), Marino Ballena National Park (ALVARADO & FERNÁNDEZ 2005), and Caño Island (GUZMÁN 1988). Echinoderms associated with soft-bottom habitats have been less studied; the only information available is from the Gulf of Nicoya. Several authors provided a list of echinoderm species collected from this tropical estuary (MAURER & VARGAS 1983; MAURER et al. 1984) and described aspects of their population dynamics (VARGAS & SOLANO 2010). The lack of knowledge regarding echinoderm species from estuarine environments is not uncommon. ALONGI (1990) had already mentioned that the diversity of subtidal fauna inhabiting soft bottoms has been poorly studied in tropical estuaries.

Térraba-Sierpe represents one of the most important wetlands in the Central American region and contains the largest mangrove forest in Costa Rica (JIMÉNEZ 1994). It is known for its diversity of fishes (CHICAS 1995), decapods (ECHEVERRÍA-SÁENZ et al. 2003), and polychaetes (SIBAJA-CORDERO & ECHEVERRÍA-SÁENZ 2015). Moreover, this mangrove supports important local ark-clam fisheries (VEGA 1994) and is a probable nursery ground for several elasmobranch species (CLARKE et al. 2014). However, the soft-bottom habitats in brackish-waters outside Térraba-Sierpe have been poorly studied. Therefore, the present study aimed to provide an inventory

of echinoderm species associated with soft-bottom sediments in Térraba-Sierpe, providing a unique opportunity to broaden our knowledge on euryhaline echinoderms in the ETP.

MATERIALS AND METHODS

Study site

Térraba-Sierpe is an estuarine delta system located in the southern Pacific coast of Costa Rica (08°51' N, 083°33' W). The delta's two main tributaries are the Térraba and Sierpe rivers with drainage areas of approximately 5077 km² and 790 km², respectively (see UMAÑA et al. 2015). This estuary probably presents a strong degree of connectivity with nearby coral reefs at Caño Island, Marino Ballena, and Corcovado (QUESADA-ALPÍZAR & CORTÉS 2006).

Annual mean precipitation in Térraba-Sierpe oscillates between 1500–6000 mm (ROJAS 2011). Suspended sediments and nutrient concentration increase during the rainy season, accompanied by a decrease in salinity (LIZANO et al. 2001; UMAÑA & SPRINGER 2006). Brackish waters have been detected in demersal habitats off the estuaries during the rainy season (PICADO 2015). The primary productivity in the estuarine region is low, with the highest values recorded in sites with high marine influence ($0.79 \pm 0.50 \text{ gCm}^{-2}$) (UMAÑA et al. 2015). More recently, mangrove tree mortality has been detected along the seaward zone, probably related to changes in sea level and sediment dynamics (LIZANO 2015).

Data collection

Sampling was conducted on a monthly basis from March 2013 to January 2014 in areas off Sierpe and Coronado estuaries at two depth levels: 5–10 m and 15–20 m (Figure 1; Table 1). The sampling was carried out alternating between the two estuaries during each month. There were three sampling stations at each depth level (Figure 1; Table 1). At each station a 20-minute tow was conducted using an artisanal trawl (1.27 cm cod-end mesh and 7 m mouth opening). Bottom salinity was measured using a SeaBird 19 Plus V2 SeaCAT profiler CTD. All collected specimens were stored on ice, transported

to the laboratory of the Centro de Investigación en Ciencias del Mar y Limnología (CIMAR) in San José, where they were preserved in 70% ethanol. In this sampling and in the same area, parallel surveys on fish fauna were carried out using gill nets (9 cm mesh size) (Figure 1; Table 1). Moreover, fishing bottom long-lines (50 m length, 50 hooks, baited with sardines) were placed in the same area including depths up to 50 m (Figure 1; Table 1). An octocoral with brittle stars was tangled in a gill net and one starfish was caught in a bottom long-line feeding on the bait. These echinoderms were also included in this list of species.

Species were identified according to GRANJA-FERNÁNDEZ (2009) and GRANJA-FERNÁNDEZ et al. (2014) for Ophiuroidea; CASO (1979, 1987, 1994) and SOLÍS-MARÍN et al. (2014) for Asteroidea; CASO (1980) for Echinoidea; and SOLÍS-MARÍN et al. (2009) for Holothuroidea. Identification of voucher asteroid specimens was corroborated by Dr. Francisco A. Solís-Marín, and ophiuroids by Dr. Rebeca Granja-Fernández. Voucher specimens of each species were deposited at the echinoderm collection of the Museum of Zoology of Universidad de Costa Rica (MZUCR). Sampling permit (No. 181-2013-SINAC) was provided by SINAC-MINAET.

RESULTS

Echinoderms were present in 23 of the 66 trawls (34.8%). Bottom salinity at sampling sites ranged from 25 to 34 parts per thousand (Table 1). A total of 225 specimens of echinoderms were recorded in four classes, four orders, six families, six genera, and nine species as listed below.

Class Asteroidea de Blainville, 1830

Order Paxillosida Perrier, 1884

Family Luidiidae Sladen, 1889

- Luidia columbia* (Gray, 1840)
Luidia columbia GRAY (1840): 183. — SOLÍS-MARÍN et al. (2014): 58.
- Luidia brevispina* — LÜTKEN (1871): 288.
- Luidia marginata* — KOEHLER (1911): 17.
- Petalaster columbia* — GRAY (1840): 183.

Table 1. Information about depth, salinity, gear type used, and geographic coordinates of the sampling locations off Coronado and Sierpe estuaries in Térraba-Sierpe mangrove, southern Pacific coast of Costa Rica.

Station	Gear	Estuary	Depth range (m)	Mean salinity (ppt)	Latitude	Longitude
1	Trawl	Coronado	5–10	27.6	09°03'23.5" N	083°39'42.4" W
2	Trawl	Coronado	5–10	27.6	09°02'47.6" N	083°39'12.3" W
3	Trawl	Coronado	5–10	26.2	09°02'12.9" N	083°38'42.3" W
4	Trawl	Coronado	15–20	31.5	09°01'32.7" N	083°38'32.6" W
5	Trawl	Coronado	15–20	33.4	09°02'11.1" N	083°38'52.6" W
6	Trawl	Coronado	15–20	30.9	09°02'47.0" N	083°39'27.2" W
7	Trawl	Sierpe	5–10	29.9	08°45'41.1" N	083°38'50.4" W
8	Trawl	Sierpe	5–10	31.4	08°45'15.2" N	083°38'48.5" W
9	Trawl	Sierpe	5–10	31.3	08°44'46.1" N	083°38'39.5" W
10	Trawl	Sierpe	15–20	33.3	08°44'37.9" N	083°40'22.8" W
11	Trawl	Sierpe	15–20	34.2	08°45'10.5" N	083°40'25.4" W
12	Trawl	Sierpe	15–20	33.6	08°46'02.5" N	083°40'31.6" W
13	Gill net	Sierpe	5–10	25.1	08°46'59.0" N	083°37'22.0" W
14	Long-line	Coronado	40–50	34.2	09°01'51.3" N	083°41'47.9" W

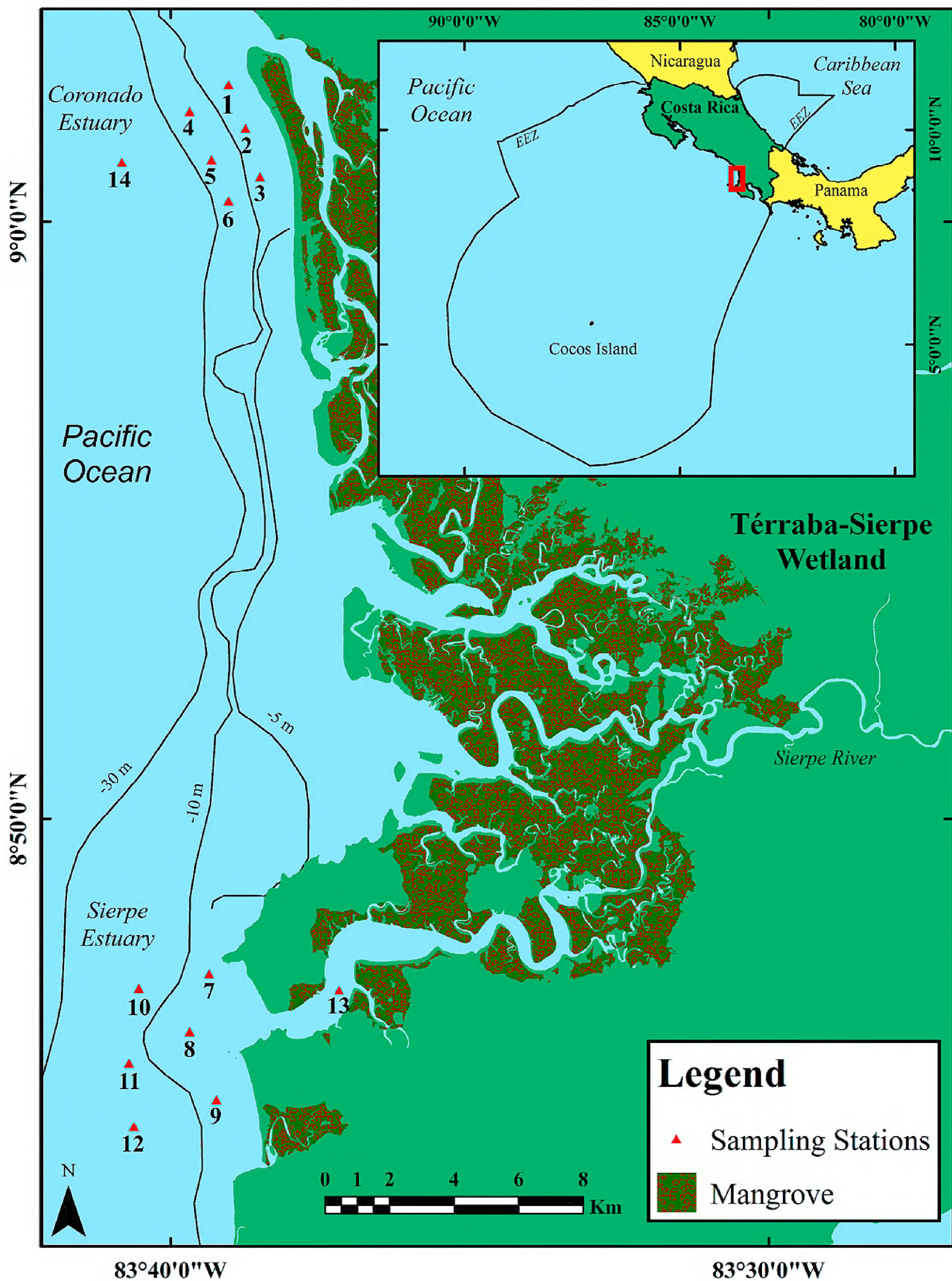


Figure 1. Study area in the Térraba-Sierpe mangrove, southern Pacific coast of Costa Rica, showing trawling sampling stations off Coronado and Sierpe estuaries at two depth levels: 5–10 m and 15–20 m. Stations 13 and 14 were sampled with a gill net and a bottom long-line, respectively.

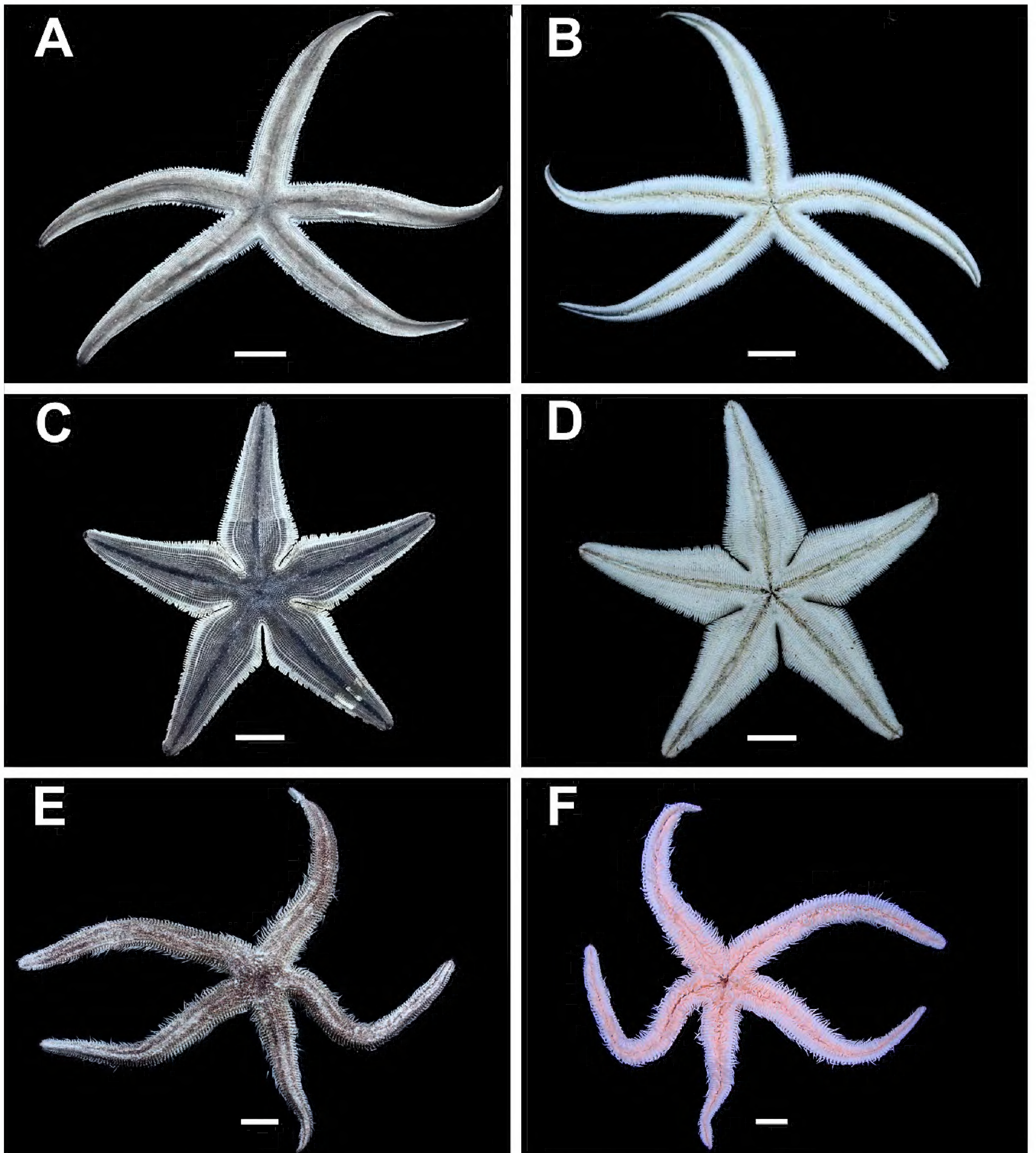


Figure 2. **A:** *Luidia columbia*, dorsal view. **B:** *L. columbia*, ventral view. **C:** *Luidia latiradiata*, dorsal view. **D:** *L. latiradiata*, ventral view. **E:** *Luidia superba*, dorsal view. **F:** *L. superba*, ventral view. Scale bar: 2 cm.

Material examined. Table 2; Figure 2A, B.

Body flattened, slightly depressed in the middle of the disc. Oral plates with one terminal spine. Arms long and slender, sharpening at the distal end. Both sides of arms with three rows of large paxillar zones, square-shaped. Middle region of arms and disc with small paxillar zones. Each inferomarginal plate with three spines, arranged in a characteristic marginal row. Each ambulacral plate with four spines. Each angle of man-

dible displays a set of 10–12 teeth.

Most of the specimens were collected in June 2013 from a single trawl at the 5–10 m depth level in Coronado estuary. New record for Costa Rica.

Luidia latiradiata (Gray, 1871)

Luidia latiradiata GRAY (1871): 136. — CASO (1945): 463; BLAKE (1972): 306.

TABLE 2. List of echinoderm species, number of specimens, locality, depth range and voucher number, recorded in waters off Térraba-Sierpe mangrove, southern Pacific coast of Costa Rica. Localities are represented by C = Coronado; S = Sierpe. New records for Costa Rica = *.

Species	Number of specimens	Locality	Depth range (m)	Station	Voucher number
* <i>Luidia columbia</i> (Gray, 1840)	82	C, S	6–20	2, 3, 6, 9	MZUCR-1107, MZUCR-1111, MZUCR-1112, MZUCR-1119
* <i>Luidia latiradiata</i> (Gray, 1871)	12	C, S	6–10	2, 3, 8, 9	MZUCR-1120, MZUCR-1121, MZUCR-1122
* <i>Luidia superba</i> A.H. Clark, 1917	3	C, S	7–42	6, 14	MZUCR-1113, MZUCR-1114, MZUCR-1115
<i>Astropecten armatus</i> Gray, 1840	15	C, S	7–20	1, 4, 5, 6, 8, 9	MZUCR-1106, MZUCR-1109
<i>Astropeten regalis</i> Gray, 1840	22	C	6–10	1, 2, 3	MZUCR-1110, MZUCR-1118
<i>Diopederma daniana</i> (Verrill, 1867)	7	C, S	5–20	4, 8	MZUCR-1123, MZUCR-1124
<i>Ophiothela mirabilis</i> Verrill, 1867	56	S	10	13	MZUCR-1116
<i>Encope micropora</i> Agassiz, 1841	2	C, S	8.0	3, 9	MZUCR-1108,
<i>Holothuria</i> (<i>Semperothuria</i>) <i>languens</i> Selenka, 1867	1	S	8.3	9	MZUCR-1105

Platasterias latiradiata — GRAY (1871): 136.

Material examined. Table 2; Figure 2C, D.

Thin, depressed body with five broader rays near proximal ends, gradually narrowing towards blunt distal ends, narrow in their insertion with disc determining deep indentations between them. Margins of rays with a closed series of semi-cylindrical spines with blunt ends. Upper marginal plates, abortive, represented by paxillae. Simple papillae.

We found some specimens of the porcelain crab *Minyocerus*

kirki Glassell, 1938 (probably as epibionts) on the surface of some specimens of *L. latiradiata*. New record for Costa Rica.

Luidia superba A.H. Clark, 1917

Luidia superba A.H. CLARK (1917): 171. — DOWNEY & WELLINGTON (1978): 375; SOLÍS-MARÍN et al. (2014): 64.

Material examined. Table 2; Figure 2E, F.

Arms large and sturdy, that sharpens towards the edge with a blunt point. Arms remarkably longer and larger compared to

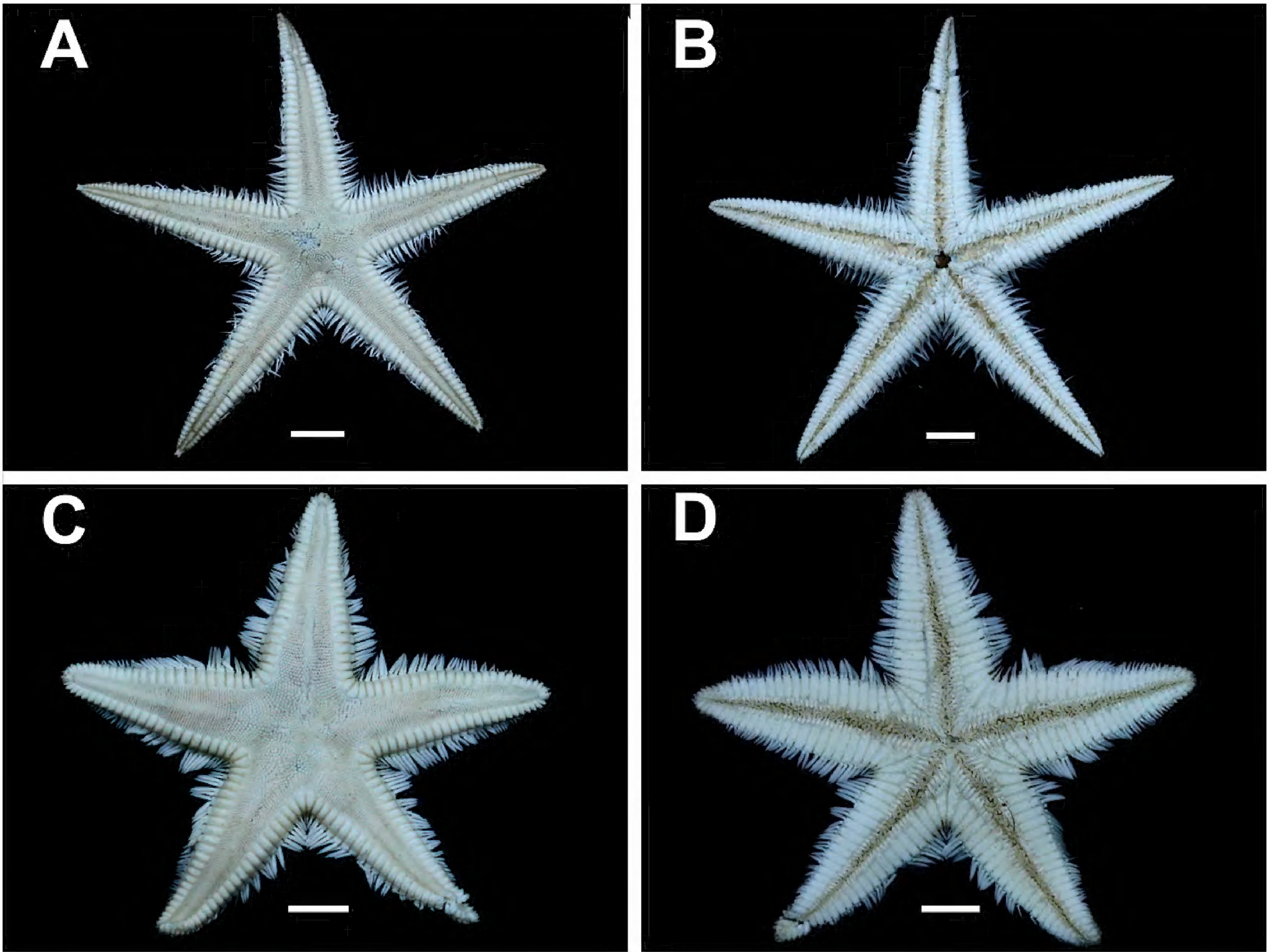


Figure 3. **A:** *Astropecten armatus*, dorsal view. **B:** *A. armatus*, ventral view. **C:** *Astropecten regalis*, dorsal view. **D:** *A. regalis*, ventral view. Scale bar: 2 cm.

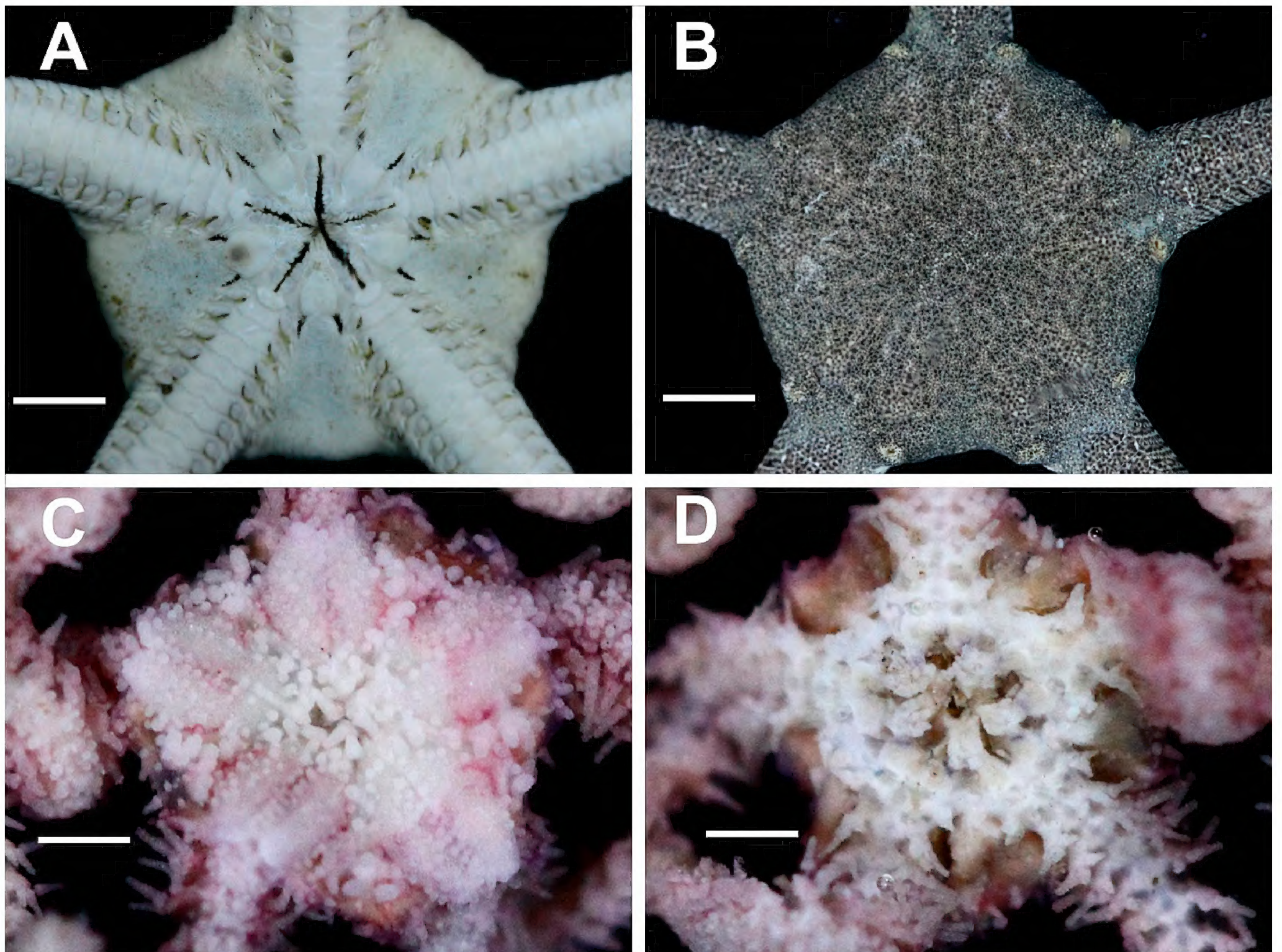


Figure 4. **A:** *Diopederma daniana*, dorsal view. **B:** *D. daniana*, ventral view. **C:** *Ophiothela mirabilis*, dorsal view. **D:** *O. mirabilis*, ventral view. Scale bar: 5 mm in **A** and **B**; 2 mm in **C** and **D**.

other *Luidia* species. Adambulacral plates with one thin spine, saber-shaped, followed by one analogous spine, longer and robust but less curved. Conical spines arranged irregularly and zigzag on paxillae of third and fourth row of the edge of arms. Tube feet well developed and turgid, without suction cups. Mouth plates narrow, with 11 spines along the middle suture.

One specimen was caught feeding on sardine bait from a bottom long-line. New record for Costa Rica.

Family Astropectinidae Gray, 1840

Astropecten armatus Gray, 1840

Astropecten armatus GRAY (1840): 181. — SOLÍS-MARÍN et al. (2014): 68.

Material examined. Table 2; Figure 3A, B.

Supramarginal plates with two parallel series of spines. Wide, large and granular marginal plates. Basal paxillae with 5–12 peripheral spines and 1–3 central spines. Madreporite striated with deep and irregular grooves.

Astropecten regalis Gray, 1840

Astropecten regalis GRAY (1840): 181. — SOLÍS-MARÍN et al. (2014): 72.

Astropecten paleatus — GRUBE (1866): 61.

Astropecten spatuliger — PERRIER (1875): 376.

Material examined. Table 2; Figure 3C, D.

Body flattened, with wide arms that sharpen towards the points. Abactinal radial surface with medial protuberance and two longitudinal hollows. Supramarginal plates with very small granuliform spines. Spine-free interradius. Madreporite presents longitudinal grooves. Inferomarginal plates with robust and corrugated spines.

Class Ophiuroidea Gray, 1840

Order Ophiurida Müller & Troschel, 1840

Family Ophiodermatidae Ljungman, 1867

Diopederma daniana (Verrill, 1867)

Diopederma danianum VERRILL (1867): 254. — GRANJA-FERNÁNDEZ (2009): 33.

Diopederma axiologum — H.L. CLARK (1913): 206.

Ophiura daniana — VERRILL (1867): 254.

Material examined. Table 2; Figure 4A, B.

Body compressed dorso-ventrally. Disc covered by fine granulation, reaching base of arms. Radial shields long, oval,



Figure 5. A: *Encope micropora*, dorsal view. **B:** *E. micropora*, ventral view. Scale bar: 2 mm.

separated and partially covered. Dorsal plates twice as long as wide and convex. Ventral plates of arms concave, twice as wide as long. Ten spines on each arm, with the most dorsal ones being the smallest. Nude, triangular and concave angular oral shields. Ten or eleven cylindrical oral papillae on each side of jaw.

Family Ophiotrichidae Ljungman, 1867

Ophiothela mirabilis Verrill, 1867

Ophiothela mirabilis VERRILL (1867): 268. — GRANJA-FERNÁNDEZ et al. (2014): 116.

Material examined. Table 2; Figure 4C, D.

Disk covered by scattered grains of different sizes. Oral and adoral shields appear to be fused, forming a continuous ring; covered by skin. Tentacle scales absent. Six arm spines with well-developed hooks at tip, with third one being the longest. Color is mainly rosaceous, with variations within pale pink and purplish tones.

All specimens of *O. mirabilis* were collected living on a colony of the octocoral *Leptogorgia laxa* Hickson, 1928 that was caught with a gill net. Many individuals showed regenerated structures.

Class Echinoidea Leske, 1778

Order Clypeasteroidea A. Agassiz, 1872

Family Mellitidae Stefanini, 1912

Encope micropora L. Agassiz, 1841

Encope micropora AGASSIZ (1841): 50. — CASO (1980): 56.

Encope occidentalis — VERRILL (1867): 309.

Material examined. Table 2; Figure 5A, B.

Test thin and fragile. The apex of test near extremity of odd ambulacra. Interambulacral lunulae remarkably small and variable in shape, compared with other species from the ETP. Anterior border of interambulacral lunulae closer to distal border of posterior petals than to center of abactinal system.

Class Holothuroidea de Blainville, 1834

Order Aspidochirotida Grube, 1840

Family Holothuriidae Burmeister, 1837

Holothuria (Semperothuria) languens Selenka, 1867

Holothuria (Semperothuria) languens SELENKA (1867): 335. — SOLÍS-MARÍN et al. (2009): 122.

Material examined. Table 2; Figure 6A, B, C, D.

Depressed thin cylindrical body. Mouth in terminal position with 20 tentacles. Ambulacral feet distributed in five rows, ventral surface in cylindrical shape, dorsal surface palliform shape. Spicules from body wall as small tables, with basal part generally conic and with spines. Border with a system of spines that form a double Maltese cross shape.

A total of seven species were collected in Coronado, while eight species were obtained in Sierpe (Table 2). The most common species in the sediments was *Luidia columbia* with 82 individuals. A total of 56 individuals of *Ophiothela mirabilis* were recorded from a single octocoral colony. Other common species (> 10 individuals) were *Astropecten regalis*, *A. armatus* and *L. latiradiata*. The remaining four species were relatively uncommon with less than 10 individuals.

DISCUSSION

Here we report three new records of echinoderm species for Costa Rica: *Luidia columbia*, *L. latiradiata* and *L. superba*. ALVARADO & SOLÍS-MARÍN (2013) reported 36 asteroid species for the Costa Rican Pacific. Therefore, this study reveals that asteroid species richness in the Costa Rican Pacific is leastwise 8.3% (39 species) higher than previously reported.

It is important to note the presence of the sea star *L. latiradiata*, considered a living fossil related to extinct asterozoans (FELL 1962; BLAKE 1982). This species has been reported from other environments with estuarine conditions: Chiapas, Mexico (CASO 1970); Gulf of Fonseca, El Salvador (BARRAZA & HASBÚN 2005); Corinto, Nicaragua (CASO 1970); close to Guapi River, Colombia (NEIRA & CANTERA 2005), and Gulf

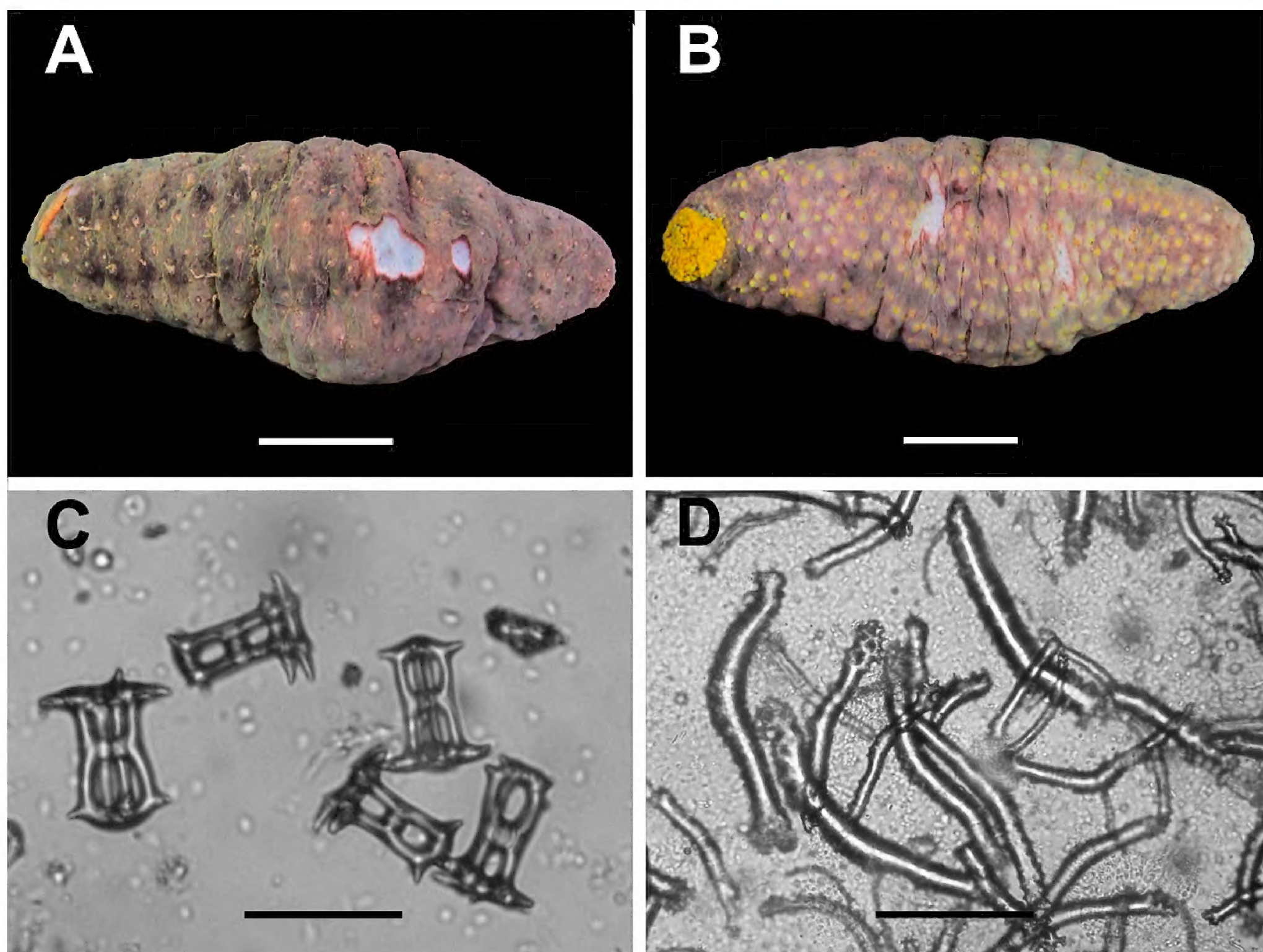


Figure 6. **A:** *Holothuria (Semperothuria) languens*, dorsal view. **B:** *H. languens*, ventral view. **C:** *H. languens*, body wall ossicles: tables. **D:** *H. languens*, tentacle ossicles: bars. Scale bar: 1 cm in **A** and **B**; **C** = 60 µm; **D** = 40 µm.

of Guayaquil, Ecuador (VILLAMAR & CRUZ 1983). The limited number of records for *L. latiradiata* in the ETP is probably due to the few studies on echinoderms in estuarine areas.

The high abundance of *Ophiothela mirabilis* was related to its association with a single octocoral colony in the middle of a mangrove channel, and it was not collected in other areas. Recently, HENDLER & BRUGNEAUX (2013) recorded this species in association with two colonies of *Leptogorgia miniata* (MILNE EDWARDS & HAIME 1857) in brackish waters of the Amazon Barrier. The presence of this ophiuroid in the Térraba-Sierpe mangrove and the previous records near the Amazon suggest that brackish environments are probably not a biogeographic barrier for *O. mirabilis*.

This is the first inventory of echinoderm species associated with soft-bottom sediments off Térraba-Sierpe. However, information on echinoderm diversity is available for the Gulf of Nicoya, another tropical estuary located further north along the Pacific coastline of Costa Rica. MAURER & VARGAS (1983) reported the presence of four ophiuroid species in subtidal soft-bottoms, which were collected by a modified Smith-McIntyre bottom grab. MAURER et al. (1984) obtained a total of nine echinoderm species, which were collected with a semi-balloon shrimp trawl: two echinoids, five ophiuroids, and two asteroids, including *A. armatus*. Despite

the geographical proximity of both areas (ca. 150 km), only *A. armatus* was recorded in both the Gulf of Nicoya and Térraba-Sierpe (MAURER & VARGAS 1983; MAURER et al. 1984; present study). The difference in species composition could be associated with the different gears used in each study and the different environmental characteristics of the two estuaries (such as productivity and salinity variations) (MAURER & VARGAS 1983; MAURER et al. 1984; PICADO 2015; UMAÑA et al. 2015).

Echinoderms are considered to be absent from brackish environments due to their stenohaline nature (STICKLE & DIEHL 1987, DAUVIN et al. 2013). However, some estuaries from different regions have shown variable echinoderm diversity. For example, the subtropical estuary of the Yangtze river in China is inhabited by four echinoderm species (CHAO et al. 2012); ten species of brittle stars were recorded in the subtropical estuarine region of Paranaguá Bay in southern Brazil (BARBOZA et al. 2015); only one species was reported in the Nahoon temperate estuary in South Africa (BURSEY & WOOLDRIGE 2002), while JOSEFSON & HANSEN (2004) mentioned 22 echinoderm species in a revision of several Danish temperate estuaries. Compared with these estuaries in other latitudes, Térraba-Sierpe has moderate echinoderm diversity (nine species).

Despite the recent increase of echinoderm studies across

Latin America (ALVARADO & SOLÍS-MARÍN 2013), there are still some areas and topics that need more attention. Recording and publishing biodiversity with high taxonomic quality contributes to improve future efforts in research, conservation, and management, and is necessary to properly assess anthropogenic or natural impacts on marine ecosystems and possible effects on the ecosystem services due to biodiversity loss (WORM et al. 2006; COSTELLO et al. 2013; ALITTO et al. 2016). There is a project to build a hydroelectric dam in the main tributary river of Térraba-Sierpe wetland (PÉREZ 2011). Dams may influence the hydrological and sedimentological dynamics, and thus influencing the coastal systems and its biodiversity (KOWALEWSKI et al. 2000). Therefore, the results of the present study complement our knowledge of Térraba-Sierpe wetland biodiversity and may contribute to future monitoring of impacts on this important mangrove area.

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LITERATURE CITED

- AGASSIZ, L. 1841. Monographies d'Echinodermes vivans et fossiles. Échinites. Famille des Clypeasteroides. Neuchâtel (Switzerland): Des Scutelles. 151 pp.
- ALITTO, R.A.S., M.L. BUENO, M. DOMENICO & M. BORGES. 2016. Annotated checklist of echinoderms from Araçá Bay, southeastern Brazil. Check List 12: 1836. <https://doi.org/10.15560/12.1.1836>
- ALONGI, D.M. 1990. The ecology of tropical soft-bottom benthic ecosystems. Oceanography and Marine Biology: An Annual Review 28: 381–496.
- ALVARADO, J.J. 2008. Seasonal occurrence and aggregation behavior of the sea urchin *Astropyga pulvinata* (Echinodermata: Echinoidea) in Bahía Culebra, Costa Rica. Pacific Science 62 (4): 579–592. <http://hdl.handle.net/10125/22733>
- ALVARADO, J.J. & A. CHIRIBOGA. 2008. Distribución y abundancia de equinodermos en las aguas someras de la Isla del Coco, Costa Rica (Pacífico Oriental). Revista de Biología Tropical 56 (Suppl. 2): 99–111. <http://revistas.ucr.ac.cr/index.php/rbt/article/view/27010>
- ALVARADO, J.J. & C. FERNÁNDEZ. 2005. Equinodermos del Parque Nacional Marino Ballena, Pacífico, Costa Rica. Revista de Biología Tropical 53 (Suppl. 3): 275–284. <http://revistas.ucr.ac.cr/index.php/rbt/article/view/26785>
- ALVARADO, J.J. & F.A. SOLÍS-MARÍN. 2013. Echinoderm research and diversity in Latin America. Berlin: Springer-Verlag Berlin Heidelberg. 658 pp.
- ALVARADO, J.J. & J. CORTÉS. 2009. Echinoderms; pp. 421–433, in: I.S. WEHRTMANN & J. CORTÉS (eds.). Marine Biodiversity of Costa Rica, Central America. Monographie Biologicae 86. Berlin: Springer and Business Media B.V.
- ALVARADO, J.J., E. BARRAZA & T.I. SANCHO-MEJÍAS. 2013. Central America echinoderms: diversity, ecology and future perspectives; pp. 67–106, in: J.J. ALVARADO & F.A. SOLÍS-MARÍN (eds.). Echinoderm research and diversity in Latin America. Berlin: Springer-Verlag Berlin Heidelberg.
- APPELTANS, W., S.T. AHYONG, G. ANDERSON, M.V. ANGEL, T. ARTOIS, N. BAILLY, R. BAMBER, et al. 2012. The magnitude of global marine species diversity. Current Biology 22: 2189–2202. <https://doi.org/10.1016/j.cub.2012.09.036>
- BARBOZA, C.A., C.C. MARTINS & P.C. LANA. 2015. Dissecting the distribution of brittle stars along a sewage pollution gradient indicated by organic markers. Marine Pollution Bulletin 100: 438–444. <https://doi.org/10.1016/j.marpolbul.2015.08.008>
- BARRAZA, J.E. & C.R. HASBÚN. 2005. Los equinodermos (Echinodermata) de El Salvador. Revista de Biología Tropical 53(Suppl. 3): 139–146. <http://revistas.ucr.ac.cr/index.php/rbt/article/view/26772>
- BENÍTEZ-VILLALOBOS, F., E. CASTILLO-LORENZANO & G.S. GONZÁLES-ESPINOSA. 2008. Listado taxonómico de los equinodermos (Echinodermata: Asteroidea y Echinoidea) de la costa de Oaxaca en el Pacífico sur mexicano. Revista de Biología Tropical 56(Suppl. 3): 75–81. <http://revistas.ucr.ac.cr/index.php/rbt/article/view/27080>
- BIRKELAND, C. 1989. The influence of echinoderms on coral reef communities; pp. 1–79, in: M. JANGOUX & J.M. LAWRENCE (eds.). Echinoderm studies. Amsterdam: Balkema.
- BLAKE, D.B. 1972. Sea star *Platasterias*: ossicle morphology and taxonomic position. Science 176: 306–307. <https://doi.org/10.1126/science.176.4032.306>
- BLAKE, D.B. 1982. Somasteroidea, Asteroidea, and the affinities of *Luidia* (*Platasterias*) *latiradiata*. Palaeontology 25: 167–191.
- BURSEY, M. & T. WOOLDRIGE. 2002. Diversity of benthic macrofauna of the flood-tidal delta of the Nahoon estuary and adjacent beach, South Africa. African Zoology 37: 231–246. <http://hdl.handle.net/10520/EJC17832>
- CASO, M.E. 1945. Modificación de la familia Luidiidae Verrill. Las subfamilias nuevas de la familia Luidiidae y observaciones acerca de *Platasterias latiradiata*. Anales del Instituto de Biología, Universidad Nacional Autónoma de México 26(2): 459–473.
- CASO, M.E. 1970. Contribución al conocimiento de los Asterozoa de México. Situación taxonómica actual. Morfología externa y datos ecológicos de *Platasterias latiradiata* Gray. Anales del Instituto de Biología 41: 1–62.
- CASO, M.E. 1979. Los equinodermos de la Bahía de Mazatlán, Sinaloa; pp. 197–368, in Instituto de Investigaciones del Mar y Limnología (ed.). Contribución 152 del Centro del Mar y Limnología – Universidad Nacional Autónoma de México 6.
- CASO, M.E. 1980. Los equinoideos del Pacífico de México parte tercera – Orden Clypeasteroidea. Mexico: Universidad Nacional

- Autónoma de México. 252 pp.
- CASO, M.E. 1987. Asteroideos, ofiuroides y equinoideos de la Bahía de Mazatlán, Sinaloa. Publicaciones Especiales del Instituto de Ciencias del Mar y Limnología 11: 1–214.
- CASO, M.E. 1994. Estudio morfológico, taxonómico, ecológico y distribución geográfica de los asteroideos colectados durante las campañas oceanográficas Cortés 1, 2, 3. Publicaciones Especiales del Instituto de Ciencias del Mar y Limnología 12: 1–111.
- CHAO, M., Y. SHI, W. QUAN, X. SHEN, C. AN, O. YUAN & H. HUANG. 2012. Distribution of benthic macroinvertebrates in relation to environmental variables across the Yangtze river estuary, China. *Journal of Coastal Research* 28: 1008–1019. <https://doi.org/10.2112/JCOASTRES-D-11-00194.1>
- CHICAS, F.A. 1995. Distribución, diversidad y dinámica poblacional de la ictiofauna comercial de la Reserva Forestal Térraba-Sierpe, Puntarenas [M.Sc. dissertation]. San Pedro: Universidad de Costa Rica. 114 pp.
- CLARK, H.L. 1913. Echinoderms from Lower California, with descriptions of new species. *Bulletin of the American Museum of Natural History* 32(8): 185–236.
- CLARK, H.L. 1917. Hawaiian and other Pacific Echini. The Echinoneidae, Nucleolitidae, Urechinidae, Echinocorythidae, Calymnidae, Pourtalesiidae, Palaestomatidae, Aeropsidae, Palaeopneustidae, Hemiasteridae, and Spatangidae. *Memoirs of the Museum of Comparative Zoology* 46(2): 91–283.
- CLARK, H.L. 1948. A report on the Echini of the warmer eastern Pacific, based on the collections of the Velero III. *Allan Hancock Pacific Expeditions* 8: 225–352.
- CLARKE, T.M., M. ESPINOZA, & I.S. WEHRTMANN. 2014. Reproductive ecology of demersal elasmobranchs from a data-deficient fishery, Pacific of Costa Rica, Central America. *Fisheries Research* 157: 95–105. <https://doi.org/10.1016/j.fishres.2014.04.003>
- COSTELLO, M.J., W.K. MICHENER, M. GAHEGAN, Z.-Q. ZHANG & P.E. BOURNE. 2013. Biodiversity data should be published, cited, and peer reviewed. *Trends in Ecology & Evolution* 28: 454–461. <https://doi.org/10.1016/j.tree.2013.05.002>
- DAUVIN, J.-C., Y. MÉAR, A. MURAT, E. POIZOT, S. LOZACH & K. BERYOUNI. 2013. Interactions between aggregations and environmental factors explain spatio-temporal patterns of the brittlestar *Ophiothrix fragilis* in the eastern Bay of Seine. *Estuarine, Coastal and Shelf Science* 131: 171–181. <https://doi.org/10.1016/j.ecss.2013.07.005>
- DEICHMANN, E. 1941. The Holothurioidea collected by the Velero III during the years 1932 to 1938. Part I. Dendrochirota. *Allan Hancock Pacific Expeditions* 8: 61–195.
- DEICHMANN, E. 1958. The Holothurioidea collected by the Velero III and IV during the years 1932 to 1954. Part II. Aspidochirota. *Allan Hancock Pacific Expeditions* 11: 253–349.
- DOWNEY, M.E. & G.M. WELLINGTON (1978). Rediscovery of the giant sea-star *Luidia superba* A.H. Clark in the Galapagos Islands. *Bulletin of Marine Science* 28(2): 375–376.
- ECHEVERRÍA-SÁENZ, S., R. VARGAS & I.S. WEHRTMANN. 2003. Diversity of decapods inhabiting the largest mangrove system of the Pacific Costa Rica. *Nauplius* 11(2): 91–97.
- FELL, H.B. 1962. *Platasterias latiradiata*. The University of Kansas Paleontological Contributions 6: 1–16.
- GRANJA-FERNÁNDEZ, M.R. 2009. Los ofiuroides (Echinodermata: Ophiuroidea) de Oaxaca [BA dissertation]. Mexico, Oaxaca: Universidad del Mar. 77 pp.
- GRANJA-FERNÁNDEZ, R., F.A. SOLÍS-MARÍN, F. BENÍTEZ-VILLALOBOS, M.D. HERRERO-PÉREZRUL & A. LÓPEZ-PÉREZ. 2015. Checklist of echinoderms (Echinodermata) from the southern Mexican Pacific: a historical review. *Revista de Biología Tropical* 63 (Suppl. 2): 87–114. <http://revistas.ucr.ac.cr/index.php/rbt/article/view/23131>
- GRANJA-FERNÁNDEZ, R., M.D. HERRERO-PÉREZRUL, R.A. LÓPEZ-PÉREZ, L. HERNÁNDEZ, F.A. RODRÍGUEZ-ZARAGOZA, R.W. JONES & R. PINEDA-LÓPEZ. 2014. Ophiuroidea (Echinodermata) from coral reefs in the Mexican Pacific. *ZooKeys* 406: 101–145. <https://doi.org/10.3897/zookeys.406.6306>
- GRAY, J.E. 1840. A synopsis of the genera and species of the class Hypostoma (*Asterias* Linnaeus). *Annals of the Magazine of Natural History* 6(36): 175–184.
- GRAY, J.E. 1871. Description of *Platasterias*, a new genus of Astropsectinidae from Mexico. *Proceedings of the Zoological Society of London* 1871: 136–137.
- GRUBE, A. E. 1866. Einige neue Seesterne des hiesigen zoologischen Museums. *Jahresbericht der Schlesischen Gesellschaft für Vaterländische Kultur* 43: 59–61.
- GUZMÁN, H.M. 1988. Distribución y abundancia de organismos coralinos de la Isla del Caño, Costa Rica. *Revista de Biología Tropical* 36: 191–207. <http://revistas.ucr.ac.cr/index.php/rbt/article/view/23686>
- GUZMÁN, H.M. & J. CORTÉS. 1992. Cocos Island (Pacific of Costa Rica) coral reefs after the 1982–83 El Niño disturbance. *Revista de Biología Tropical* 40: 309–324. <http://revistas.ucr.ac.cr/index.php/rbt/article/view/24547>
- GUZMÁN, H.M. & J. CORTÉS. 2007. Reef recovery 20 years after the 1982 – 1983 El Niño massive mortality. *Marine Biology* 151: 401–411. <https://doi.org/10.1007/s00227-006-0495-x>
- HENDLER, G. & S. BRUGNEAUX. 2013. New records of brittle stars from French Guiana: *Ophiactis savignyi* and the alien species *Ophiorthela mirabilis* (Echinodermata: Ophiuroidea). *Marine Biodiversity Records* 6: 1–5. <https://doi.org/10.1017/S1755267213000845>
- HERTLEIN, L.G. 1963. Contribution to the biogeography of Cocos Island, including a bibliography. *Proceedings of the California Academy of Sciences* 32: 123–235.
- HONEY-ESCAÑÓN, M., F.A. SOLÍS-MARÍN & A. LAGUARDA-FIGUERAS. 2008. Echinodermos (Echinodermata) del Pacífico Mexicano. *Revista de Biología Tropical* 56 (Suppl. 3): 57–73. <http://revistas.ucr.ac.cr/index.php/rbt/article/view/27079>
- JANGOUX, M. 1982. Food and feeding mechanisms: Asteroidea; pp. 117–159, in: M. JANGOUX & J.M. LAWRENCE (eds.). *Echinoderm nutrition*. Amsterdam: Balkema.
- JANGOUX, M. & J.M. LAWRENCE. 1982. *Echinoderm nutrition*. Amsterdam: Balkema. 700 pp.
- JIMÉNEZ, J.A. 1994. Los manglares del Pacífico de Centroamérica. Heredia: Fundación Editorial UNA. 336 pp.
- JOSEFSON, A.B. & J.L.S. HANSEN. 2004. Species richness of benthic macrofauna in Danish estuaries and coastal areas. *Global Ecology and Biogeography* 13: 273–288. <https://doi.org/10.1111/j.1466-822X.2004.00091.x>
- KOEHLER, R. 1911. Description de quelques asteries nouvelles. *Revue Suisse de Zoologie* 19: 1–21.
- KOWALESKI, M., G.E. AVILA, K.W. FLESSA & G.A. GOODFRIEND. 2000. Dead delta's former productivity: two trillion shells at the mouth of the Colorado River. *Geology* 28: 1059–1062. <http://geology.gsapubs.org/content/28/12/1059>
- LAWRENCE, J.M. 1987. A functional biology of echinoderms. London: Croom Helm. 340 pp.
- LESSIOS, H.A. 2005. Echinoids of the Pacific waters of Panama: status of knowledge and new records. *Revista de Biología Tropical* 53(Suppl. 3): 147–170. <http://revistas.ucr.ac.cr/index.php/rbt/article/view/26773>
- LESSIOS, H.A., B.D. KESSING, G.M. WELLINGTON & A. GRAYBEAL. 1996. Indo-Pacific echinoids in the tropical eastern Pacific. *Coral Reefs* 15: 133–142. <https://doi.org/10.1007/BF01771904>
- LIZANO, O., J. AMADOR & R. SOTO. 2001. Caracterización de manglares de Centroamérica con sensores remotos. *Revista de Biología Tropical* 49: 331–340. <http://revistas.ucr.ac.cr/index.php/rbt/article/view/26339>
- LIZANO, O.G. 2015. La dinámica oceanográfica frente al Humedal

- Nacional Terraba-Sierpe y su relación con la muerte del manglar. *Revista de Biología Tropical* 63(Suppl. 1): 29–46. <http://revistas.ucr.ac.cr/index.php/rbt/article/view/23092>
- LÜTKEN, C. 1871. Fortsatte kritiske og beskrivende Bidrag til Kundskab om Søstjernerne (Asteriderne). *Videnskabelige Meddelelser fra den naturhistoriske Forening i Kjöbenhavn* 3: 227–308.
- MAURER, D. & J.A. VARGAS. 1983. Benthic studies in the Gulf of Nicoya, Costa Rica. Delaware: University of Delaware, College of Marine Studies. 105 pp.
- MAURER, D., C. EPIFANIO, H. DEAN, S. HOWE, J.A. VARGAS, A. DITTEL & M.M. MURILLO. 1984. Benthic invertebrate of a tropical estuary: Gulf of Nicoya, Costa Rica. *Journal of Natural History* 18: 47–61. <https://doi.org/10.1080/00222938400770071>
- Menge, B.A. 1982. Effects of feeding on the environment; pp. 521–551, in: M. JANGOUX & J.M. LAWRENCE (eds.). *Echinoderm nutrition*. Amsterdam: Balkema.
- NEIRA, R. & J.R. CANTERA. 2005. Composición taxonómica y distribución de las asociaciones de equinodermos en los ecosistemas litorales del Pacífico colombiano. *Revista de Biología Tropical* 53(Suppl. 3): 195–206. <http://revistas.ucr.ac.cr/index.php/rbt/article/view/26776>
- PAWSON, D.L. 2007. Phylum Echinodermata. *Zootaxa* 1668: 749–764. <http://www.mapress.com/zootaxa/2007f/zt01668p764.pdf>
- PÉREZ, B. 2011. Reflexiones sobre el proyecto hidroeléctrico El Diquís y sus impactos sociales en las comunidades de Terraba, Buenos Aires y Ceibo. *Revista Reflexiones* 90: 1021–1209. <http://revistas.ucr.ac.cr/index.php/reflexiones/article/view/14493>
- PÉREZ-RUZAFÁ, A., J.J. ALVARADO, F.A. SOLÍS-MARÍN, J.C. HERNÁNDEZ, A. MORATA, C. MARCOS, M. ABREU-PÉREZ, et al. 2013. Latin America echinoderm biodiversity and biogeography: patterns and affinities; pp. 511–542, in J.J. ALVARADO & F.A. SOLÍS-MARÍN (eds.). *Echinoderm research and diversity in Latin America*. Berlin: Springer-Verlag Berlin Heidelberg.
- PERRIER, E. 1875. Révision de la Collection de Stellérídes du Museum d'Histoire Naturelle de Paris. Paris: Reinwald. 384 pp.
- PICADO, J. 2015. Distribución espacial y temporal de la salinidad en la columna de agua del sector estuarino del Humedal Nacional Terraba-Sierpe, Costa Rica. *Revista de Biología Tropical* 63(Suppl. 1): 75–96. <http://revistas.ucr.ac.cr/index.php/rbt/article/view/23097/23351>
- QUESADA-ALPÍZAR, M., & J. CORTÉS. 2006. Los ecosistemas marinos del Pacífico sur de Costa Rica: estado del conocimiento y perspectivas de manejo. *Revista de Biología Tropical* 54: 101–145. <http://revistas.ucr.ac.cr/index.php/rbt/article/view/26832>
- ROJAS, N. 2011. Estudio de cuencas hidrográficas de Costa Rica: cuenca del Río Grande de Terraba. San José: Instituto Meteorológico Nacional. 21 pp.
- SELENKA, E. 1867. Beiträge zur Anatomie und Systematik der Holothurien – Zeitschrift für Wissenschaftliche Zoologie 17 (2): 291–374, pls 17–20.
- SIBAJA-CORDERO, J.A. & S. ECHEVERRÍA-SÁENZ. 2015. Polychaetes associated with decaying wood in the Terraba mangrove, South Pacific, Costa Rica. *Revista de Biología Tropical* 63 (Suppl. 1): 61–74. <http://revistas.ucr.ac.cr/index.php/rbt/article/view/23096/23349>
- SOLÍS-MARÍN, F.A., A. LAGUARDA-FIGUERAS, P. ESTRADA-RODRÍGUEZ, M.B.I. HONEY-ESCAÑÓN, C. MARTÍN-CAO-ROMERO & A. DURÁN-GONZÁLEZ. 2014. Los asteroideos (Echinodermata: Asteroidea) del Golfo de California. Mexico: SEMARNAT, INECC. 190 pp.
- SOLÍS-MARÍN, F.A., J.A. ARRIAGA-OCHOA, A. LAGUARDA-FIGUERAS, S.C. FRONTANA-URIBE & A. DURÁN-GONZÁLEZ. 2009. Holothuroideos (Echinodermata: Holothuroidea) del Golfo de California. Mexico: Instituto de Ciencias del Mar y Limnología-Universidad Nacional Autónoma de México y Comisión Nacional para el Conocimiento y Uso de la Biodiversidad. 177p.
- SOLÍS-MARÍN, F.A., A. LAGUARDA-FIGUERAS, A. DURÁN-GONZÁLEZ, C.G. AHEARN & J. TORRES. 2005. Equinodermos (Echinodermata) del Golfo de California, México. *Revista de Biología Tropical* 53 (Suppl. 3): 123–137. <http://revistas.ucr.ac.cr/index.php/rbt/article/view/26770/26955>
- STICKLE, W.B. & W.J. DIEHL. 1987. Effects of salinity on echinoderms; pp. 235–285, in: M. Jangoux and J.M. Lawrence (eds.). *Echinoderm studies*, 2nd volume. Rotterdam: Balkema.
- UMAÑA, G. & M. SPRINGER. 2006. Variación ambiental en el río Grande de Terraba y algunos de sus afluentes, Pacífico Sur de Costa Rica. *Revista de Biología Tropical* 54 (Suppl. 1): 265–272. <http://revistas.ucr.ac.cr/index.php/rbt/article/view/26850/27025>
- UMAÑA, G., J. ACUÑA, J. GARCÍA, F. AGÜERO, J.C. ZÚÑIGA, E. GÓMEZ & J. PICADO. 2015. Productividad primaria en el Humedal Nacional Terraba-Sierpe, Costa Rica. *Revista de Biología Tropical* 63(Suppl. 1): 9–28. <http://revistas.ucr.ac.cr/index.php/rbt/article/view/23091/23341>
- VARGAS, J.A. & S. SOLANO. 2011. On *Mellitella stokesii* and *Amphipholis geminata* (Echinodermata), from an intertidal flat in the upper Gulf of Nicoya estuary, Pacific, Costa Rica. *Revista de Biología Tropical* 59 (1): 193–198. <http://revistas.ucr.ac.cr/index.php/rbt/article/view/3189>
- VEGA, A.J. 1994. Estructura de población, rendimiento y épocas reproductivas de *Anadara* spp. (Bivalvia; Arcidae) en la Reserva Forestal Terraba-Sierpe, Puntarenas, Costa Rica, con recomendaciones para su manejo [M.Sc. dissertation]. San Pedro: Universidad de Costa Rica. 118 pp.
- VERRILL, A.E. 1867. Notes on Radiata in the Museum of Yale College with descriptions of new genera and species – II. Notes on the echinoderms of Panama and the west coast of America, with descriptions of a new genus. *Transaction of the Connecticut Academy of Arts and Sciences* 1(2): 251–322.
- VILLAMAR, F. & M. CRUZ. 1983. Presencia de *Platasterias latiradiata* Gray en aguas ecuatorianas. *Acta Oceanográfica del Pacífico* 2: 169–177. <http://www.inocar.mil.ec/web/index.php/publicaciones/file/20-presencia-de-platasterias-latiradiata-gray-en-aguas-ecuatorianas>
- WORM, B., E.B. BARBIER, N. BEAUMONT, J.E. DUFFY, C. FOLKE, B.S. HALPERN, J.B.C. JACKSON, et al. 2006. Impacts of biodiversity loss on ocean ecosystem services. *Science* 314: 787–790. <http://dx.doi.org/10.1126/science.1132294>
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